THE INTERLOCKING MECHANISMS WHICH ARE FOUND IN CONNECTION WITH THE ELYTRA OF COLEOPTERA.

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It is a matter of common knowledge that the elytra of most beetles are co-adapted with each other and with the body of the insect. Yet it appears that no one has ever described these co-adaptations in any detail in spite of the fact that several very interesting mechanical devices are here brought into use. The attention of the senior author of this paper was called to them while studying the muscular system of beetles. At that time he discovered that a small muscle, attached to the meta-episternum, had been erroneously thought to be an expiratory muscle and that in reality it operated a mechanism for hooking the edge of the elytron to the body at this place (Breed, :03, page 332).

Writings on the subject seem to be limited to a few general statements in text-books. Packard ('98) says that the wing cases of beetles join along their dorsal suture like the valves of a mussel shell. He further states that there is an interlocking of the elytra with the scutellum, citing the stag-beetle as an example. He also finds that the elytra of stag-beetles interlock with each other by means of a groove, and that this is the method usually found in beetles; but that in some cases the joining is after the method of two cog-wheels. He likens these devices to the two methods most used by the cabinet-maker in joining boards.

Sharp ('99) says that in most beetles the elytra are fitted together and to the sides of the body, except at the tip, but he gives no further explanation. He also states that sometimes the tips of the elytra are fastened to the body, but that this occurs only in the cases where the abdomen is not entirely covered by them. He says further that in the blister beetles, which include the Cantharides and the Meloides, the elytra are not co-adapted with the abdomen. The former are winged but the latter are so-called

apterous forms, with elytra overlapping at the base. The same author says that in some species the elytra are soldered together along the suture. The degree of firmness of the joining varies even in specimens of the same species, probably depending on the age of the individual.

1. Material and Methods.

The material used was *Lachnosterna fusca* Auct., the June-bug or May-beetle, *Thymalus marginicollis* Chevr., a small beetle which lives in the common shelf fungus of white birch, and *Tenebrio molitor* Linn., the meal beetle.

The method used in examining the co-adaptations of the elytra in the two larger beetles was to take specimens hardened in alcohol and cut off the posterior part of the body, wings and elytra with a razor. Then the remainder of the insect was placed under a low power of the microscope in such a position that the face of the cross section could be viewed. In some cases it was found advantageous to embed the whole beetle in paraffin first. Then the desired section was cut free-hand with a razor, after which a part or the whole of the paraffin was dissolved away and the cut face examined with a microscope. When studying the separate elytra, thin sections were cut in pith in the same way that botanical sections are so often prepared. In this way perfect, though rather thick, sections were obtained, whereas microtome sections were badly broken.

In the case of *Thymalus*, which is a small beetle with a comparatively thin cuticula, it was found possible to prepare series of microtome sections of the entire insect. These series show both the interlocking along the dorsal suture and the musculus episternalis with its related parts. By selecting young imagines of *Lachnosterna* and *Tenebrio* and sectioning only a portion of the body, series of microtome sections of these beetles were prepared which show the musculus episternalis and its related parts.

2. Observations.

There are commonly found in beetles four devices for fastening the elytra in place, all of which may be utilized in one animal. The fastening may be accomplished :

1. By a co-adaptation of the elytra along the dorsal suture.

2. By means of a groove on the dorsal face of the metathorax into which the swollen inner edges of the elytra fit.

3. By slipping the anterior edges of the elytra under the scutellum and hooking them (*a*) on to the scutellum, or (*b*) on to the metathorax. Pressure derived from the retracted prothorax may aid in keeping these edges in position.

4. By hooking the anterior lateral edges of the elytra over ridges or into grooves on the lateral faces of the metathorax.

(*a*) *Interlocking Mechanisms found in Lachnosterna.*

Lachnosterna fusca is one of the lamellicorn beetles. The head, prothorax and elytra show in dorsal view, together forming a broad oval outline. The elytra almost cover the abdomen, the exposed part being curved downward in such a way that it cannot be seen from above. The abdomen is shortened and rounded, and the elytra curve sharply downward at the sides and posteriorly.

The first three of the methods of interlocking mentioned above are used in *Lachnosterna.* The hooking mechanism of the fourth method is present, but is not functional.

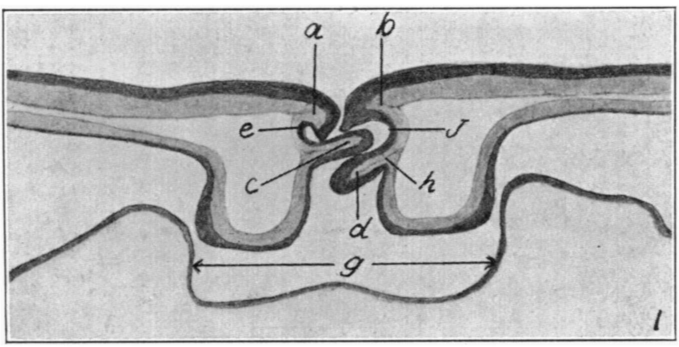

FIG. 1. Mid-dorsal portion of the cross section of the elytra and metathorax of *Lachnosterna*, showing the adaptation of the elytra to each other along the dorsal suture and to the metathoracic groove. $\times 75$.

1. The method of joining along the dorsal suture is shown in Fig. 1, which represents a cross section of the mid-dorsal region of the elytra. In this case the elytra are nearly as they would be when the elytra were firmly closed, and are partially slipped into

the underlying metathoracic groove. When the elytra are separated, the cross section of the right one appears as in Fig. 2. The ridge *b* is stiff, but the ridge *d*, being narrower at *h*, acts like a spring. When the two elytra are drawn together, the ridge *c* strikes the ridge *d* and bends it downward. The ridge *c* then

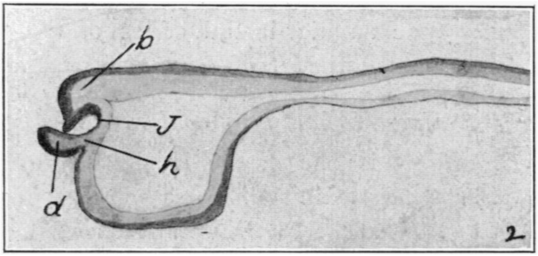

FIG. 2. Cross section of the mid-dorsal portion of the right elytron of *Lachnosterna*, showing the relation of the two ridges when the two elytra are not locked together. $\times 75$.

slips into the groove *j*, and *d* springs back, holding *c* tightly in the groove *j*. By comparing Fig. 2 (a figure of the right elytron) with that of the left elytron represented in Fig. 1, it will be seen that the two are remarkably alike when the elytra are separated. No conception of the way in which they interlock was formed until the two were studied in their natural relations by the method

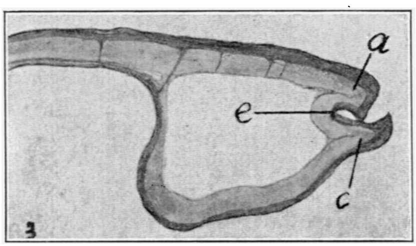

FIG. 3. Cross section of the mid-dorsal edge of the left elytron of *Lachnosterna* as seen in the extreme anterior portion. $\times 75$.

described above. The ridges and grooves along the dorsal suture have essentially the same form throughout the length of the elytra but the joining is the firmest along the anterior third of the suture. Figs. 3 and 4 represent the region close to the point of the scutellum. Figs. 1 and 2 show the structure at a point

about one millimeter back of the scutellum. Figs. 5 and 6 show cross sections of the elytra from near the middle region. In all ot the specimens examined, the ridge on the left elytron hooks into the groove on the right elytron.

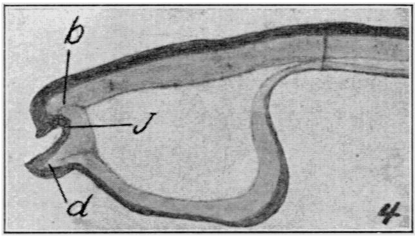

FIG. 4. Similar to Fig. 3. Right elytron. $\times$ 75.

2. Figs. 1 to 6 show the thickenings of the lower face of each elytron along the mid-dorsal edge in cross section. Figs. 1 and 2 show the form of these thickenings in the metathoracic region. Beneath these thickenings there is a groove along the metathorax, well stiffened with chitin, into which the thickenings fit tightly when they are interlocked. This groove is seen in cross section at *g*, in Fig. 1. The thickenings of the elytra in the

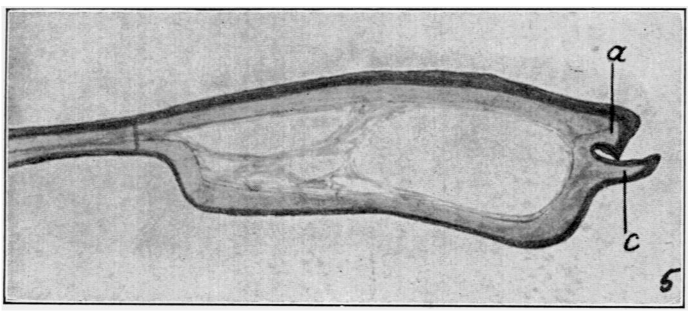

FIG. 5. Cross section of the mid-dorsal thickening of the left elytron of *Lachnosterna* as seen near the posterior end of the elytron. $\times$ 75.

anterior part of the suture are more abrupt than elsewhere, the contour of the under side of the elytron being here S-shaped in cross section (Figs. 3 and 4), so that the thickenings hook into the metathoracic groove, which is slightly wider in its ventral than in its dorsal part.

3. The metathoracic groove widens in its anterior portion, so that the entire groove has the form of a Y with its arms projecting forward. The triangular scutellum lies in the opening between the arms of the Y. In closing the elytra, their anterior

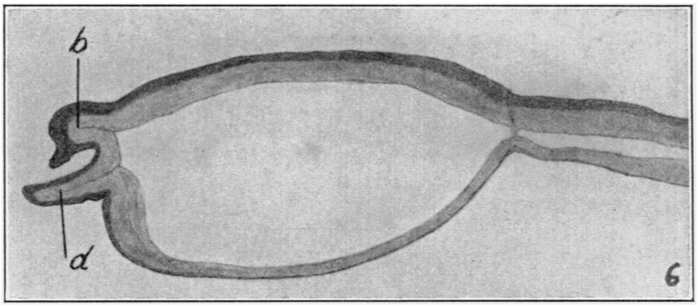

FIG. 6. Similar to Fig. 5. Right elytron. $\times 75$.

edges slip under the diagonal edges of the scutellum and hook over the ridges made by the diverging arms of the Y. The thickening along the edge of the elytron at this point has still

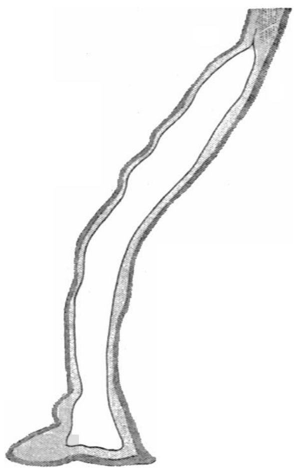

FIG. 7. Cross section of the lateral edge of the right elytron of *Lachnosterna*. $\times 150$.

more the form of a hook than those shown in Figs. 3 and 4. The interlocking is therefore very firm in this region, especially as the downward pressure of the scutellum aids in resisting any

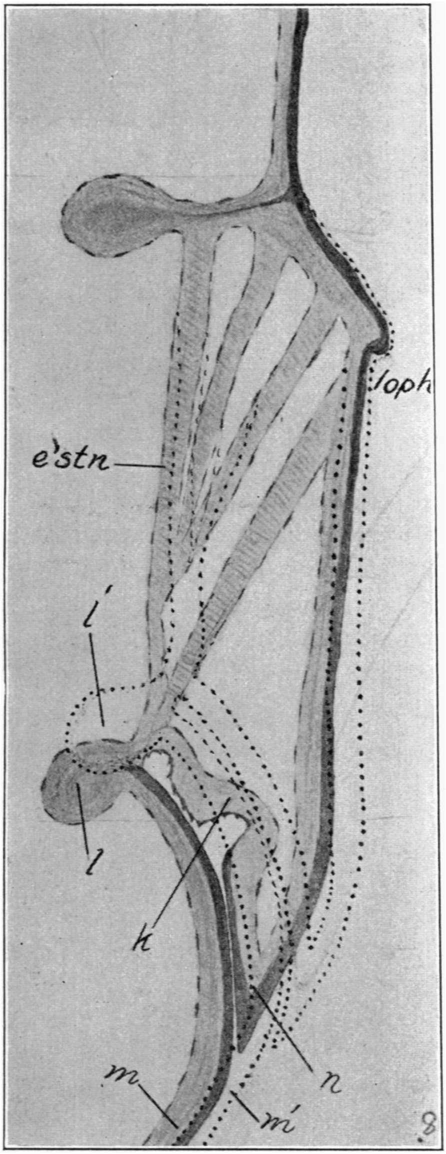

FIG. 8. Lateral portion of a cross section of the metathorax of *Lachnosterna*, showing the parts affected by the contraction of musculus episternalis. × 150.

forcible detachment of the elytra. This pressure of the scutellum is supplemented by the retraction of the prothorax against the

mesothorax. There is no interlocking of the elytra with the scutellum in this beetle.

4. The elytra are not fastened along the lateral faces of the metathorax, although a rudimentary hook (Fig. 7) is found along the anterior lateral edge of each elytron. A corresponding ridge hooking downward (Fig. 8, *loph.*) is found on the meta-episternum, a short distance below the origin of the musculus episternalis (*e'stn.*).

The probable method by which this hook would be operated is shown in Fig. 8. The dotted lines show the position of the movable parts when the muscle is contracted. The ridge represented in cross section at l is drawn up to the position l', and the flexible band k is straightened. The meta-sternum m is drawn upward and outward to the position m', thus forcing the ventral edge n of the episternum outward. A dissection of the muscular system of several beetles has shown that the lower attachment of the musculus episternalis is along a straight line, while the upper attachment is arched somewhat like the gable of a house. This form gives firmness and affords reason for believing that it is the lower attachment of this muscle which moves when the muscle contracts. Further proof of this is furnished by the triangular form of this muscle in longitudinal section (Fig. 8, *e'stn.*). Thus the dorsal end of this muscle serves as origin, while the ventral end is insertion. The movement of the ventral edge of the episternum outward would cause the slant of the ridge (*loph.*) to change slightly. If there were a functional hook present on the edge of the elytron, the change in position due to the contraction of this muscle would be sufficient to release the elytron or to allow it to return to its place.

However, since the hook present on the elytron is rudimentary, this muscle is apparently functionless though it must have been functional in some ancestral form. The muscle has not degenerated as completely as have the chitinous structures in connection with it. The degeneration of the lateral hooking mechanism may be accounted for by the highly developed interlocking mechanisms in the other parts of the body. The dorsal suture, the meta-thoracic groove, and the fastening under the scutellum furnish ample means for holding the elytra firmly in place.

(*b*) *Interlocking Mechanisms found in Thymalus.*

Thymalus marginicollis is one of the trogositid beetles; it has the same general form as a lady beetle, but it is still better adapted in form of body for clinging to a surface after the manner of a limpet. The dorsal view of the body is a nearly perfect broad oval showing simply the pronotum and elytra with a small portion of the head. The flange on the edge of the elytron (seen at *f* in Fig. 9) fits closely against the surface on which the beetle is resting. The adult beetles are commonly found during the

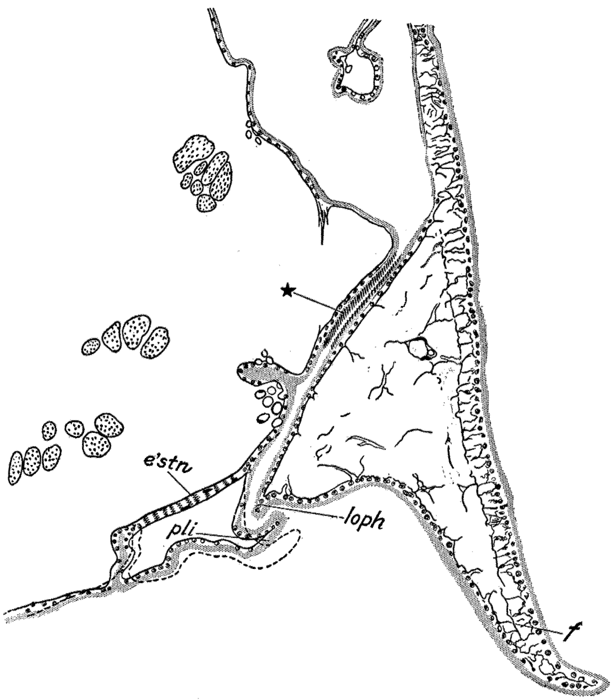

FIG. 9. *Thymalus.* Copied from Breed, :03. Similar to Figs. 8 and 12. × 100.

early part of the summer lurking about the shelf fungi which have served their larvæ as food.

The four general methods of fastening the elytra in place which were mentioned above are all functional in this beetle. The coadaptation between the body and the elytra is so perfect that it is nearly impossible to unclasp the elytra in a dead specimen without tearing them.

1. The co-adaptation along the dorsal suture is shown in Figs. 10 and 11. The lower ridge *d* (Fig. 11) of the right elytron fits into the groove *e*, the interlocking in this case being just the reverse of that found in *Lachnosterna* (Fig. 1). Moreover, there is no clasp arrangement, the ridge *c* remaining as rigid as the others. The suture would not hold together if there were not a lateral stress exerted upon the elytra. In the anterior region,

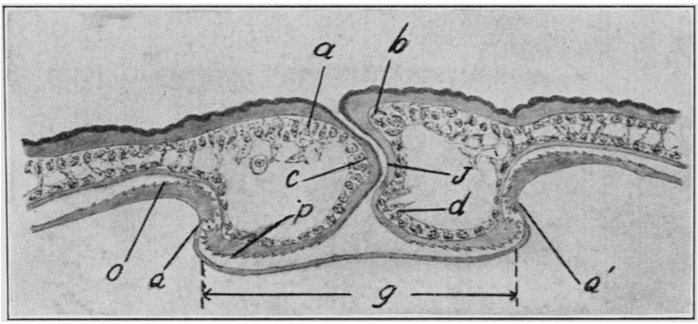

FIG. 10. Mid-dorsal region of a cross section of the elytra and metathorax of *Thymalus*, showing the adaptation of the elytra to each other and to the metathoracic groove. × 130.

the ridges become very feeble and in the most anterior sections (see Fig. 10) a ridge *c* on the left elytron fits into a groove *i* on the right elytron thus reversing the condition found in the middle and the posterior regions.

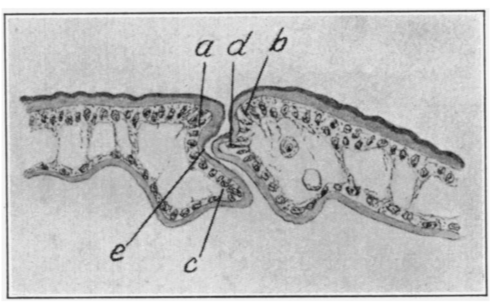

FIG. 11. Mid-dorsal region of a cross section of the elytra of *Thymalus* in the region immediately posterior to the metathorax. × 130.

2. Fig. 10 shows in cross section the thickened edges of the elytra, and the metathoracic groove (*g*) into which they hook.

The hooks are so pronounced that they make a very perfect joining, which holds the edges of the elytra together along the dorsal suture. This arrangement is made more effective by rows of minute chitinous teeth (*o*, *p*) which in the cross section resemble saw teeth. These are so directed that they keep the elytra from slipping laterally when they are being drawn together, by interlocking at the points *q* and *q'* they assist in keeping the wing covers perfectly co-adapted when at rest.

3. The interlocking of the elytra of *Thymalus* along their anterior edges is very much as it is in *Lachnosterna*. The principal difference is that the inner anterior corners of the elytra slip under the scutellum more than in the June beetle and the pronotum fits against the anterior edges more firmly.

4. The method of fastening the elytra to the meta-episternum is shown in Fig. 9. This figure is copied from Breed (:03, Fig. 13, Plate 6). A description of the mechanism which it illustrates is to be found on page 332 of the paper referred to. There is a ridge (*pli.*) on the face of the episternum, lying between the attachments of the musculus episternalis (*e'stn.*). The contraction of this muscle causes the ridge (*pli.*) to take the position indicated by the dotted line, thus freeing the ridge (*loph.*) on the elytron and allowing the latter to be raised. In like manner the musculus episternalis contracts when the elytron returns to rest and its immediate relaxation causes the latter to be securely fastened in its place. At the point marked by a star (*) there is found on the inner face of the elytron a row of minute teeth directed upward. A similar series of teeth pointing downward is found on the body wall opposite. These teeth interlock and assist in keeping the elytron in place. A few small teeth are also present on the inner face of the ridge (*pli.*).

The dorsal suture is thus kept intact by the combined working of the dorsal metathoracic groove and this lateral hooking arrangement. The combination of these two devices produces the stress which holds the mid-dorsal edges of the elytra in the positions shown in Figs. 10 and 11.

(*c*) *Interlocking Mechanisms found in Tenebrio.*

The common meal beetle is one of the Tenebrionidæ. It may be found abundantly through the summer months in granaries and mills, or flying into houses. It is an elongated beetle whose head, prothoracic and body regions are distinctly separated from each other in dorsal view.

The elytra of this beetle are not very firmly interlocked either with the body or with each other. All four of the methods previously mentioned are used in this interlocking.

1. The mid-dorsal edges of the elytra are co-adapted much as in *Lachnosterna* (cf. Fig. 1). However minute teeth are found along the dorsal surface of the ridge *c*, which fit in with similar teeth on the ventral side of the ridge *b*. In three of the individuals examined the ridge on the right elytron fitted into a groove on the left elytron while in two others the reverse was true.

2. The dorsal groove along the metathorax is both shallow and narrow. Minute interlocking teeth are developed on the thickened edges of the elytra and on the metathorax, as in *Thymalus* (cf. Fig. 10). These teeth are more blunt than those in *Thymalus* and do not form as perfect an interlocking device.

3. The inner anterior corners of the elytra slip under the diagonal edges of the scutellum, showing very perfect co-adaptation at this point. The prothorax does not fit tightly against the elytra and is not used in holding them in place.

4. The most interesting of these co-adaptations is that of the lateral edges of the elytra with the episternum. As seen in Fig. 12, which represents the right lateral portion of a cross section through this region viewed from behind, there are numerous teeth on the inner surface of the elytron at *s*, which interlock with teeth on the body wall at *s'*. Apparently the teeth at *t* and *t'* do not interlock because: (1) long movable hairs are found along the small ridge *u*, which would interfere with this action; (2) the shape of the body would prevent it; (3) the teeth themselves do not seem stout enough to serve for this interlocking. The action of the teeth at *s* and *s'*, working in connection with the co-adaptations along the dorsal suture, would cause a strain on the elytra which would hold them in place.

The triangular area embraced between the straight dotted lines shows the form of the episternal muscle projected on the plane of the section. The origin of the musculus episternalis is along the entire dorsal boundary of the meta-episternum. Most of its fibers take their origin from the thickened ridge *v*. The insertion is by means of a tendon which attaches to the anterior portion of the ventral edge of the episternum. The entire muscle is thus

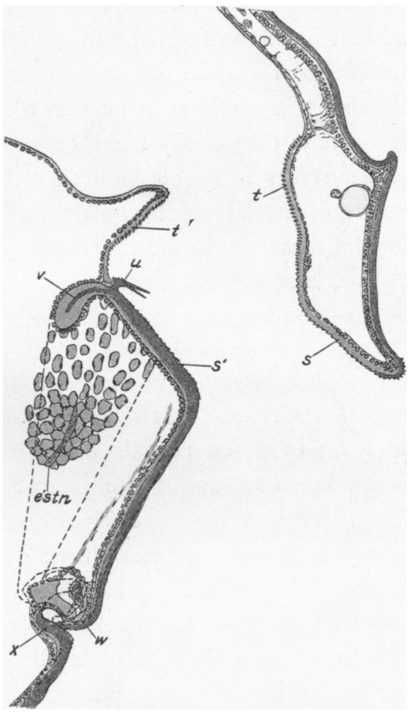

FIG. 12. Lateral portion of a cross section of the metathorax of *Tenebrio*, showing the parts affected by the contraction of musculus episternalis. $\times 75$.

somewhat fan-shaped in side view. It is only in sections anterior to the one shown that the fibers are cut so as to show their full length in any one section.

It is difficult to determine the exact method by which the muscle operates. The structure of the suture to which this muscle attaches is remarkably complex and entirely unlike that found in the two beetles just described. The structure shown in Fig. 12 is typical for all of the sections of this suture The teeth shown

along the outer surface of the region *w* and the surface *x* show a better development in the section figured than in most of the sections.

There are at least two reasons for thinking that the condition figured is one which represents the contracted or nearly contracted state of this muscle. These reasons are: (1) the cross striations of the muscle appear as they do in contracted fibers, (2) the position of the parts affected. A dotted outline has been drawn (not shown satisfactorily in the figure) which indicates the probable position of these parts when the muscle relaxes. This relaxation would cause the teeth at *s* and *s'* to grip each other firmly if the elytron had previously been brought near enough the body for these surfaces to touch each other.

The most effective of the interlocking devices in this beetle are the mid-dorsal metathoracic groove, the slipping of the corners of the elytra under the scutellum, and the interlocking of these teeth along the meta-episternum.

(*d*) *Comparison.*

A comparison of the devices which are used by these beetles in holding their elytra in place reveals a close similarity in all cases, except in the interlocking of the lateral edges with the meta-episternum. Here the most striking dissimilarity exists. In all of the beetles which we have examined, a muscle has been found which originates along the dorsal edge of the episternum, and is inserted on the suture which marks the ventral boundary of this plate. This has been called the musculus episternalis. In one case (*Lachnosterna*) this muscle is apparently functionless since the chitinous structures which it operates are so degenerate that they no longer interlock. In *Thymalus* this muscle operates an upward hooking ridge, in *Tenebrio* a series of downward hooking teeth.

This dissimilarity of structure with its consequent differences in the method of operation is made possible by varying flexibilities of the chitinous cuticula.

It would be interesting to know how many other variations of these structures may be present among beetles. The three species examined were chosen at random and it does not seem possible

that all of the variations have been discovered. Some light might be thrown on the relationships of the various families of beetles to one another if more were known about these interlocking devices.

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BIBLIOGRAPHY.

Breed, R. S.

:03 The Changes which Occur in the Muscles of a Beetle, Thymalus marginicollis Chevr., during Metamorphosis. Bull. Mus. Comp. Zoöl., Harvard Coll., Vol. XL., pp. 317–382, 7 pls., 1 fig.

Packard, A. S.

'98 A Text-book of Entomology. New York, xvii + 729 pp., 654 figs.

Sharp, D.

'99 Insects. Part II. The Cambridge Natural History, Vol. VI. London, xii + 626 pp., 293 figs.

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